

DROUGHT AND HEAT STABILITY OF THE PHOTOSYNTHETIC APPARATUS IN BREAD WHEAT AND IN *AEGILOPS* SPECIES

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Abstract

The responses of CO₂ gas exchange, and heat stability were examined in two wheat (*Triticum aestivum* L.) cultivars and in *Aegilops* genotypes originating from habitats with different annual rainfalls and daily temperatures. Desiccation in soil pots resulted in moderate water loss in *Ae. biuncialis* MvGB 377, 382 and *Ae. bicornis* MvGB 585, parallel with a high degree of stomatal closure and significant decrease in the net CO₂ fixation (*A*), while in *Ae. tauschii* MvGB 605, 589 stomatal conductance (*g_s*) and *A* remained relatively high in the desiccation period, and parallel with this *g_s* and *A* were more tolerant to decrease in RWC than in wheat cultivars and in the above-detailed *Aegilops* genotypes. In spite of this, the decrease of RWC was fast and considerable in *Ae. biuncialis* MvGB 642, *Ae. speltoides* MvGB 1042, 624, and in *Ae. tauschii* MvGB 426 with a low degree of stomatal closure but *A* was more tolerant to water loss, especially in *Ae. speltoides* MvGB 1042. On the other hand, higher water deficit (RWC ~75%, 10-14 days drought treatment) resulted in a significant increase in the thermal stability of PS II for wheat and for some *Aegilops* genotypes. The results indicate that some *Aegilops* genotypes originating from arid habitats have better drought and desiccation induced heat tolerance than wheat, making them appropriate for improving the heat tolerance of wheat to survive dry and hot periods in the field.

Keywords: drought stress, thermal tolerance, photosynthesis, wheat, *Aegilops sp.*

Introduction

Aegilops species with good tolerance to some major abiotic stress factors are closely related to wheat (Van Slageren 1994) and widely used as

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genetic resources for *Triticum* species (Molnár *et al.* 2004). Especially the tetraploide goat grass (*Aegilops biuncialis* L., $2n = 4x = 28$, $U^bU^bM^bM^b$) has a good drought tolerance, which makes it suitable to improve the drought tolerance of wheat (Molnár *et al.* 2004). In addition, diploide goat grasses, such as *Ae. tauschii* Coss. (DD), *Ae. bicornis* (S^bS^b) and *Ae. speltoides* Tausch. (SS) have some other advantages. As the B and D genome donors of wheat are the *Ae. speltoides* and *Ae. tauschii* genotypes, the chromosome mediated gene transfer from these species to hexaploide wheat is easier than from *Ae. biuncialis*.

Drought and heat are important biomass-limiting stress factors (Berry and Björkman 1980, Araus *et al.* 2002) in the field causing the suppression of cultivated plants in growth and in crop production (Blum *et al.* 1997). During drought the water potential (ψ), relative water content (RWC) and net photosynthetic CO_2 fixation (A) substantially decrease (Bajji *et al.* 2001, Molnár *et al.* 2004). The reduction of A partially results from the closure of stomata due to water deficit, since decrease of stomatal conductance (g_s) is the most efficient way to reduce water loss, and parallel with this the CO_2 diffusion into the leaves is restricted, resulting in a decrease in intercellular CO_2 concentration (C_i) (Cornic 2000). On the other hand, the limitation of CO_2 fixation during water deficit is also influenced by the diffusion of CO_2 from the intercellular spaces to chloroplasts (Delfine *et al.* 1999, Loreto *et al.* 2003), and by other metabolic factors such as changes in the activity of ribulose-1,5-bisphosphate-carboxylase-oxygenase (Rubisco) and perturbed regeneration of ribulose-1,5-bisphosphate, etc (Molnár *et al.* 2004).

The heat sensitivity of plants is closely connected to the thermal stability of PS II. It is more or less clear that the thermal tolerance of the photosynthetic apparatus in some higher plants is influenced by other stress factors like light (Havaux and Tardy 1996, Molnár *et al.* 1998), and by water deficit in a desiccation tolerant moss (Dulai *et al.* 2004). The study of these problems is further justified by the fact that under natural conditions high light intensity, heat stress, and water deficit occur in combination with each other: the effects of the three stress factors need to be tolerated at the same time.

In connection with the above-mentioned facts *Aegilops* species are natives in the Mediterranean and in arid or semi-arid continental regions, which are characterised by hot summers with a low amount of seasonal or annual rainfall. On the other hand, physiological acclimation features in some measure depend on the climate of the original habitat of plants (Zahireva *et al.* 2001, Bultynck *et al.* 2003). Since the vegetation period in native habitats of the examined *Aegilops* species is dry and hot, these plants had to develop various acclimation strategies to drought and to heat.

In this paper we compare some physiological responses to drought and heat in several *Aegilops* species originating from different rainfall conditions with two wheat genotypes presumably characterised by a different drought tolerance to indicate that some of them have better drought and heat tolerance than wheat, making them suitable for improving the drought and heat tolerance of wheat by intergeneric crossing, enabling it to survive the dry and hot periods in the field.

Materials and Methods

All experiments were performed on intact leaves or leaf segments of *Triticum aestivum* L. and of *Aegilops* sp. Seeds were germinated under laboratory conditions. After germination, these plants were grown in 1.5 kg soil pots in an unheated greenhouse for 5 weeks under natural sunlight. The water deficit was induced by withholding the water supply in the soil. The water status of the plants was traced by determining the relative water content (RWC).

The responses of the *in vivo* chlorophyll *a* fluorescence to heat were measured in dark-adapted leaves with a pulse amplitude modulation fluorometer (PAM 101-103, Walz, Effeltrich, Germany) as described Dulai *et al.* (1998). For the determination of the breakpoints (T_c , and T_p) of the F_0 vs. T or F_s vs. T curves the heat induction of fluorescence method was applied as described by Schreiber and Berry (1977).

The CO₂ assimilation of intact leaves was measured at saturating light intensity (1000 $\mu\text{E m}^{-2} \text{s}^{-1}$) using an infrared gas analyser (ADC LCA-2, Analytical Development Co. Ltd, Hoddesdon UK). The rates of net CO₂ fixation (A), stomatal conductance (g_s), and intercellular CO₂ concentration were determined using the equations of von Caemmerer and Faquhar (1981).

Results and discussion

Effects of drought stress on the water content of the leaves

During drought the water balance of plants changes, parallel with which the relative water content (RWC) decreases. At the same time, though not to the same degree and not with the same RWC values, a change can be observed in certain photosynthetic processes (Chaves *et al.* 1991, Lawlor and Upreti 1991, Lawlor 1995, Cornic 1994, Cornic and Massacci 1996, Bajji *et al.* 2000), in dry matter production, growth rate and crop production (Blum *et al.* 1997, Frensch 1997, Araus *et al.* 2002, Molnár *et al.* 2004). If plants are able to hold the water effectively, that is, when the water potential is kept

high in the dry period as well, they have a good chance to survive the dry period, which however does not mean that the above-mentioned processes are not susceptible to the decrease of water content.

The time dependence of RWC decrease in several *Aegilops* genotypes was considerably different from that of wheat cultivars (Fig. 1). In certain genotypes water loss is slower than in wheat, with a significant decrease of RWC only after the 9th-10th day, and their water content is significantly higher than that of wheat even at the end of the dry period (they are water-preserving). In some of these lines the originally high stomatal conductance (g_s) will significantly decrease at a slight water loss (*Ae. biuncialis* MvGB 377, 382, *Ae. bicornis* MvGB 585), and stomatal closure, as is well-known, is the most efficient way of reducing water loss (Cornic 2000). At the same time, *Ae. tauschii* MvGB 605 and 589, while efficiently keeping water, are not characterised by abrupt stomatal closure; their RWC during drought does not decrease drastically, despite the higher g_s . As opposed to the ones mentioned above, there are four lines in which water loss is faster than in wheat (*Ae. biuncialis* MvGB 642, *Ae. speltoides* MvGB 1042, 624, *Ae. tauschii* MvGB 426). In these, under normal water conditions g_s is lower than in the previous group, but decreases less with water loss and can even increase at the beginning of the desiccation period. In this latter group the net assimilation rate (A) decreases faster with time than in Mv9Kr1, but is less sensitive to the decrease of RWC than in some of the water-preserving plants (Figs 1 and 2).

Effects of drought stress on the gas exchange parameters

During water deficit stomatal closure can be observed, parallel with which stomatal conductance (g_s), the intercellular CO₂ level (C_i) and, as a result, photosynthetic CO₂ fixation decreases (Cornic 2000). As the light reactions of photosynthesis is generally influenced only by a more considerable water loss, the decrease of A during drought at a given light intensity is determined by the activity of the Calvin-Benson cycle and the CO₂ supply of the Rubisco. The CO₂ level at the active site of Rubisco (C_c) is determined by the CO₂ diffusion between the ambient CO₂ (C_a) and the active site of Rubisco. This latter is partly determined, through influencing the intercellular CO₂ level, by stomatal conductance (g_s), which decreases parallel with stomatal closure during drought (Cornic 2000). As a result, intercellular CO₂/O₂ ratio can also change, which leads to an increase of photorespiration, and thus in the decrease of CO₂-fixation is also influenced by metabolic factors.

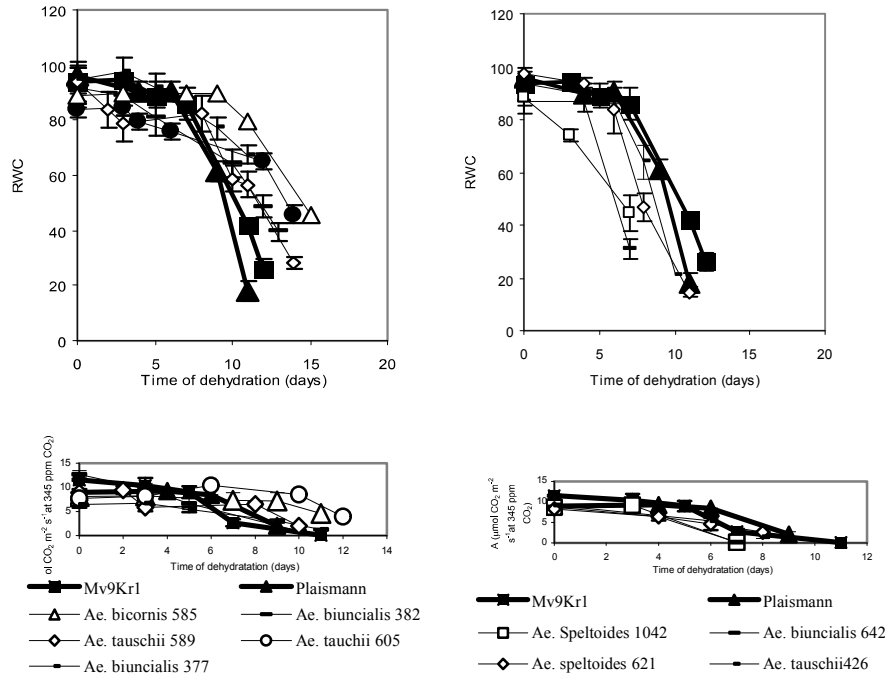


Fig. 1 Effects of drought stress on relative water content (RWC, above) and on time dependence of net CO₂ assimilation rate (A, below) at 1000 $\mu\text{E m}^{-2} \text{s}^{-1}$ light intensity for wheat and for *Aegilops* genotypes.

In Fig. 1, the time dependence of A during drought stress is represented in two groups, which correspond to the dynamics of RWC decrease. The group which efficiently keeps water during dehydration is able to maintain an acceptable level of A for a longer time, despite the fact that stomatal conductance decreases rapidly during drought treatment in some of the genotypes (*Ae. biuncialis* MvGB 377, 382, *Ae. bicornis* MvGB 585, Fig. 3). The *Ae. tauschii* MvGB 605 and 589 lines are also characterised by a similarly satisfactory A , but stomatal conductance is kept higher in these than in the others during the drought treatment, despite the fact that their water content decreases slowly, as in the genotypes with low g_s (Figs. 1 and 3). However, while CO₂ fixation in the *Ae. biuncialis* MvGB 377, 382, *Ae. bicornis* MvGB 585 lines is very sensitive to the decrease of RWC (although it decreases slowly), it remains relatively high in *Ae. tauschii* MvGB 605 and 589 even at a lower water content, and in 605 the original rate of fixation is kept up even at 65% of RWC (Fig. 2). On the other hand, in the *Aegilops* lines which are characterised by fast water loss, A decreases as rapidly, or even more rap-

idly, as in the Mv9Kr1 wheat cultivar but is less sensitive to water loss. In these lines during drought g_s decreases less, compared to the original value (Fig. 3), and in *Ae. biuncialis* MvGB 642 and *Ae. speltoides* MvGB 1042 it increases significantly at a slight RWC decrease.

Thus in these genotypes different strategies can be presumed on the basis of the changes of g_s and A during drought. When g_s is high even during water deficit, it limits carbon assimilation less. Although water loss can be relatively rapid then, dry matter production is probably acceptable and crop production can be fast. On the other hand, water preservation is probably another efficient strategy to survive dry periods.

In water-saturated C_3 plants, with environmental CO_2 concentration and corresponding C_i , at saturating light intensity, A does not reach the maximum level which is measurable at saturating CO_2 concentration (A_{max}). Water deficit-induced A decrease can result from stomatal closure or because of mesophytic conductance or metabolic factors (such as the perturbed regeneration of ribulose-1,5-bisphosphate or the inhibition of the electron transport chain etc.) In the first case, A_{max} can be restored by increasing the ambient CO_2 level, which is not possible in the case of metabolic limitation. A_{max} is restored even at low RWC values in *Ae. tauschii* MvGB 605, 589 and *Ae. speltoides* MvGB 1042 by the high ambient CO_2 level, and as a result A in these lines may be limited by the CO_2 diffusion to the intercellular spaces even at a lower water content (not shown by data).

In the *Aegilops* lines studied, on the basis of the changes of A , g_s and RWC during drought, some strategies can be assumed to have a bearing on the plants' survival of the dry period.

Drought-tolerant genotypes: they efficiently preserve water content, but g_s and A do not drastically decrease with water loss (*Ae. tauschii* MvGB 605, 589).

Water-preserving genotypes: during dehydration RWC slowly decreases, and A and g_s decrease rapidly parallel with water loss. CO_2 fixation is maintained at a reduced rate at low stomatal conductance for a longer time (*Ae. biuncialis* MvGB 377, 382, *Ae. bicornis* MvGB 585).

Water-losing genotypes: RWC decreases rapidly during dehydration. A and g_s are less sensitive to water loss (*Ae. speltoides* MvGB 1042 and several other transitory lines).

Drought-sensitive genotypes: During drought treatment water content and CO_2 fixation drop rapidly. A is very sensitive to the decreases of RWC, independently of the change of other parameters (*Ae. biuncialis* MvGB 1094).

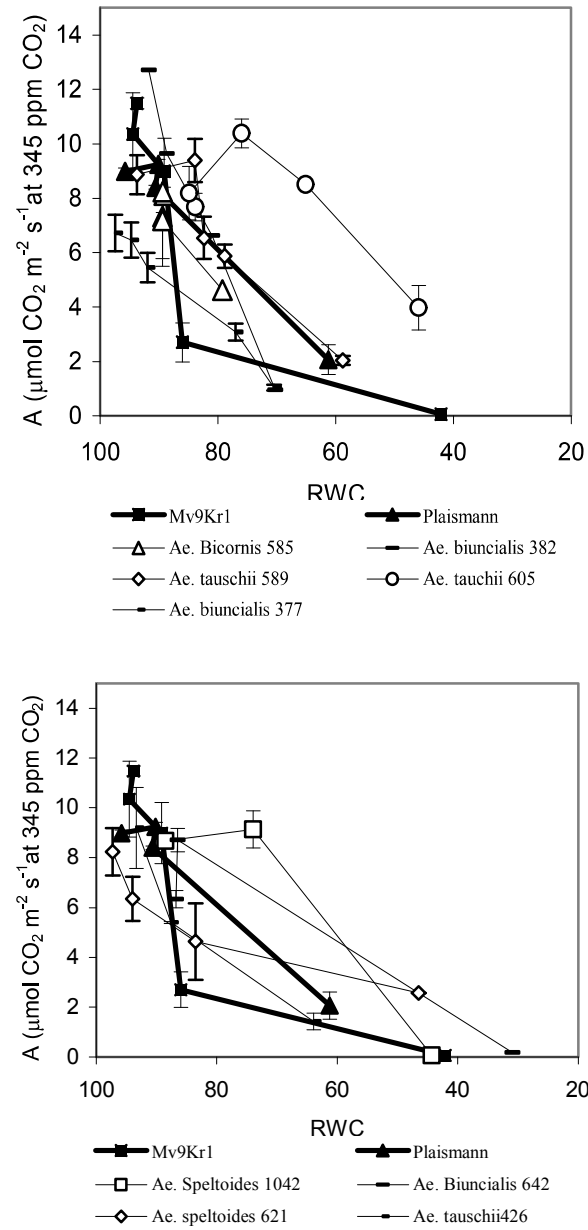


Fig. 2 Effects of decrease in relative water content (RWC) on the net CO_2 assimilation rate (A) at $1000 \mu\text{E m}^{-2} \text{s}^{-1}$ light intensity for wheat and for *Aegilops* genotypes.

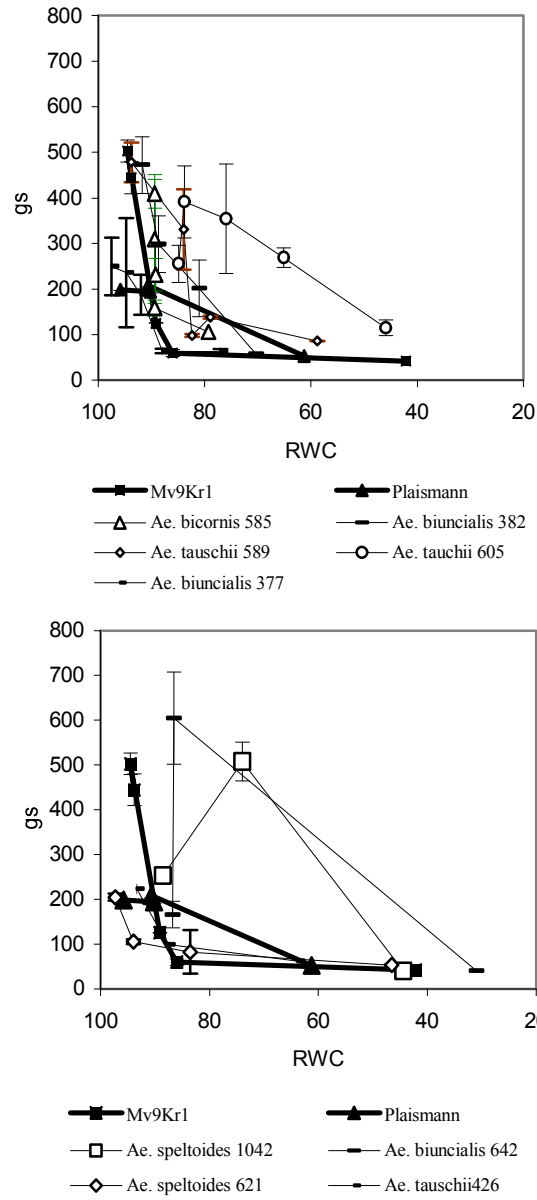


Fig. 3 Effects of decrease in relative water content (RWC) on the stomatal conductance (g_s , $\text{mmol m}^{-2} \text{s}^{-1}$) at $1000 \mu\text{E m}^{-2} \text{s}^{-1}$ light intensity for wheat and for *Aegilops* genotypes.

Heat tolerance changes of PS II during drought stress

The sensitivity of plants to heat stress is closely connected to the thermal stability of PSII, which is well characterized by the critical values of the temperature dependence of the initial fluorescence level (F_0) of dark-adapted leaves (Schreiber and Berry 1977). The heat tolerance of PSII in wheat and in *Aegilops* genotypes determined on the basis of the F_0 vs. T curves (practically in darkness) was not sufficient for tolerating such high temperatures that are peculiar to their original habitats (not shown by data) coupled with high irradiation and drought. Similarly to F_0 , the breakpoints (T_c , T_p) of temperature dependence of steady state fluorescence (F_s) – according to recent results – appropriately show the thermal stability of samples with a steady-state photosynthesis level (Molnár *et al.* 1998, Dulai *et al.* 2004). In connection with this, T_c values of F_s vs. T curves measured at moderately high AL intensity ($1000 \mu\text{E m}^{-2} \text{s}^{-1}$) are shifted towards significantly higher temperatures (42-45 °C), indicating the higher thermal tolerance of PSII for wheat cultivars and for goat grasses (not shown by data).

Table 1 Effect of water deficit on the breakpoints (T_c) of the F_s vs. T curves at $1000 \mu\text{E m}^{-2} \text{s}^{-1}$ actinic light (AL) intensity. T_{c0} , T_c values of non-stressed plants; T_{c1} , T_c values measured at the end of the dry period.

Species, genotypes	$T_{c0}(1000 \mu\text{E})$	$T_{c1} (1000 \mu\text{E})$
Mv9Kr1	44.9±0.115	49,0±0.000
Plaismann	45.3±0.115	47,5±0.500
<i>Ae. biuncialis</i> 382	44.5±0.000	49,0±0.000
<i>Ae. tauschii</i> 589	44.5±0.000	49,7±0.577
<i>Ae. tauschii</i> 605	45.0±0.000	51,0±0.500
<i>Ae. bicornis</i> 585	45.8±0.289	48,0±0.000
<i>Ae. biuncialis</i> 377	44.0±0.000	46,0±0.000
<i>Ae. biuncialis</i> 470	44.0±0.000	46,2±0.289
<i>Ae. biuncialis</i> 642	45.3±0.289	45,0±0.000
<i>Ae. biuncialis</i> 1094	45.0±0.000	48,0±0.000
<i>Ae. biuncialis</i> 1112	45.5±0.000	44,7±0.289
<i>Ae. tauschii</i> 363	41.3±1.768	40,5±3.464
<i>Ae. tauschii</i> 426	44.8±0.354	44,8±0.289
<i>Ae. speltooides</i> 1042	46.5±0.707	49,0±0.000
<i>Ae. speltooides</i> 621	43.5±0.707	44,8±0.577

However, during drought the relative water content and the activity of some photosynthetic processes decrease there are observations to the effect that in higher plants the slow dehydration of removed leaves resulted in an increase of the thermal stability of PS II (Havaux 1992). To select the promising *Aegilops* genotypes with high tolerance to heat during the drought the

thermal stability of PSII was examined. The three-day drought treatment did not effect a considerable water loss in leaves and parallel with this a significant heat-tolerance increase of PS II was not observable. Whereas heat sensitivity during the drought increased in three *Aegilops* genotypes, as a result of severe water deficit (RWC<75%), in wheat cultivars and in most goat grasses with steady-state photosynthesis at 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ AL intensity the critical values of the F_s vs. T curves were shifted significantly higher, compared to the unstressed plants (Table 1). This enhanced thermal stability was more or less also manifested by the temperature dependence of the effective quantum yield of PSII (not shown by data). These phenotypic plasticity changes (Table 1) to heat were most remarkable for three goat grasses originating from arid habitats (*Ae. biuncialis* MvGB 382, *Ae. tauschii* MvGB 589 and *Ae. tauschii* MvGB 605).

On the basis of the results presented it seems that, although parallel with different water loss and stomatal closure, *Ae. tauschii* MvGB 589, 605, *Ae. speltoides* MvGB 1042 *Ae. bicornis* MvGB 585 and *Ae. biuncialis* MvGB 382 are able to maintain a sufficient CO₂ fixation and, at the same time, a high heat tolerance of the photosynthetic apparatus during drought. These properties make them a good candidate for improving the heat and drought tolerance of wheat by intergeneric crossing, to effectively survive the forecasted dry and hot periods in the fields of central Europe.

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